

The comparison of the feeding of European perch *Perca fluviatilis* L. larvae in littoral and pelagic habitats of northern temperate lakes

Katrit Karus^{a,b*}, Matiss Zagars^a, Helen Agasild^b, Tõnu Feldmann^b, Arvo Tuvikene^b,
Linda Puncule^{a,b} and Priit Zingel^b

^a Institute for Environmental Solutions, 'Lidlauks', Priekuļu parish, 4126 Priekuļu county, Latvia

^b Centre for Limnology, Institute of Agricultural and Environmental Sciences, Chair of Hydrobiology and Fishery, Estonian University of Life Sciences, 61117 Rannu, Tartu, Estonia

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Abstract. We studied the feeding of European perch *Perca fluviatilis* L. larvae in littoral and pelagic habitats of four different lakes – one Latvian (Auciema) and three Estonian (Akste, Kaiavere, and Prossa). Altogether, 162 perch larvae (81 from both habitats) were collected to estimate the diet composition of gathered larval specimens in spring (2019) using gut content analysis via epifluorescence microscopy. Attention was paid particularly to the question how does the larval perch food composition differ in pelagic and littoral habitats. We hypothesized that the consumption of zooplankton is higher and the larval condition is better in littoral habitats. We assessed the feeding on both protozoa- (ciliates) and metazooplankton and applied multiple indices (Hurlbert's standardized niche breadth, Ivlev's selectivity and relative importance index) to evaluate, respectively, the larval fish prey importance, feeding homogeneity and strategies. The results showed that larval length and weight were slightly higher and body condition was slightly better in the lakes' littoral habitats. The feeding niche of perch larvae was narrower in the littoral, which can indicate more favourable feeding conditions in littoral than lake pelagic habitats. While the small cladocerans (*Bosmina longirostris* Müller) were generally the preferred and important food objects, ciliates were avoided and consumed only when their share in the total zooplankton biomass was >40%. However, in shortage of cladocerans, ciliates could be vitally important food objects for perch larvae.

Keywords: exogenous feeding, food selectivity, habitat, lakes, perch larvae, zooplankton.

1. INTRODUCTION

The pelagic and vegetated littoral zones of lakes serve as distinct habitats for planktivorous fish larvae. In the pelagic zone, the most relevant structuring drivers are abiotic factors (water movements, stratification, temperature, etc.), whilst in the littoral zone the most relevant structuring forces are among habitat heterogeneity created by macrophyte type and distribution patterns (Dionne and Folt 1991). Submerged macrophytes may serve as refuges for juvenile fish against piscivorous fish predation (Diehl 1993; Diehl and Eklöv 1995; Schriver et al. 1995; Okun

and Mehner 2005) as increasing complexity of macrophytes usually decreases the foraging success of predators (Winfield 1986; Stahr and Shoup 2015). At the same time, planktivorous and juvenile fish exert a strong grazing pressure on zooplankton in both habitats (Nicolle et al., 2010) but it may be slightly lower in the littoral (Diehl 1988; Persson 1993). Despite the refuge potential of macrophytes for zooplankton, comparatively few studies have examined how vegetation influences the interactions between planktivorous fish larvae and zooplankton in the lake ecosystems. Particularly, how the habitat type influences the larval fish feeding characteristics and the potential for larval condition. These relations are often hard to follow since the outcome of trophic interactions

* Corresponding author, katrit.karus@emu.ee

may vary on a large scale, depending on ever so many factors (e.g., habitat heterogeneity, density of predators and prey, feeding types and efficiencies of the predators (Jeppesen et al. 1998)).

The European perch (*Perca fluviatilis*) is a piscivorous freshwater fish common in large parts of Europe and Asia inhabiting almost all types of running and standing waters. Perch is known to spawn only in littoral and not in pelagic area of lakes. Perch produce very small larvae (hatching roughly at 5.4 mm and 0.7–0.8 mg) that are initially very fragile and vulnerable to several problems, e.g., failure of development, cannibalism, predation, starvation (Overton and Paulsen 2005) and start swimming immediately without filling their swim bladder (Urho 1996). It is generally claimed that perch larvae seek open water shortly after hatching (Persson and Greenberg 1990; Urho 1996; Persson et al. 2000; Byström et al. 2003), where they mostly stay 1–2 months (Urho 1996; Wang and Eckmann 1994), and that this shift is mainly genetic. Nevertheless, it is not entirely clear if all perch larvae seek to enter the open-water area and what percentage remains in the littoral. Urho (1996) followed perch larval distribution in L. Saarlampi and found that the shift to the pelagic zone started when larval mean size was as little as 8 mm and some gas had appeared in their swim bladder. It is not entirely clear how the larvae shift. Their dispersal may be achieved by currents but also swimming activity is proposed (Urho 1996). Of course, it must be considered that the swimming speed of perch larvae is modest – larvae under 9.5 mm sustain velocities of only <3.0 cm/sec (Houde 1969a,b).

Larval perch are generally known to migrate back to the littoral after some time spent in open water (Persson et al. 2000; Byström et al. 2003). Some authors have suggested that the majority of perch population return to the littoral habitat before reaching a total length of 19 mm (Coles 1981). Urho (1996) suggested that this migration takes place gradually when the fish have reached a length of 8 to 40 mm. There seem to be considerable differences between different lakes. In the meso-eutrophic L. Constance, this shift is not completed until perch are more than 30 to 40 mm long and have reached the juvenile stage (Wang and Eckmann 1994). It is noted that some individuals change habitat faster than others and some return to the littoral only as juveniles, spending most of their larval stage in the pelagic zone (Urho 1996). In our own former studies in L. Vörtsjärvi and Väinameri Sea (semi-enclosed Baltic Sea basin) (Zingel et al. 2012; Zingel et al. 2019a; 2019b) we have found perch larvae as small as 8–10 mm who have supposedly already returned to the littoral. At the same time, we have found 0+ perch >30 mm remaining in the open water, confirming that some individuals change habitat faster than others and there occurs a large individual variation. It is also stated that in smaller, oligotrophic lakes 0+ perch return to the littoral at the end of

the larval period, whereas in larger, eutrophic lakes the shift is delayed until the juvenile stage (Urho 1996). Suggested mechanisms behind the shift back to the shore are predation risk, resource limitation (Persson et al. 2000) and genetic predisposition.

Most scientists agree that fish year-class strength is established during the larval stadium (Hjort 1914; Yufera and Darias 2007). Main limitations at the transition to the exogenous feeding are the size of mouth gape, larval length, and immaturity/absence of some organs (e.g., air-bladder, fins, fully developed eyes) restricting swimming capacity and hunting success (Nunn et al. 2012; Yufera and Darias 2007). Faster general body development may favour earlier external feeding by perch larvae, even prior to complete exhaustion of the yolk sac (Ilina 1973; Kazanova 1953; Lankov et al. 2006). As a piscivore, perch larvae hatch with a relatively large gape size (Kurmayer and Wanzenbock 1996; Byström and García-Berthou 1999). Therefore, they incorporate larger zooplankters into their diet earlier in life and can utilize a broader resource spectrum than many other fish species (Byström and García-Berthou 1999). Our own studies (Zingel et al. 2012; Zingel et al. 2019a; 2019b) have confirmed that perch larvae can consume a wide selection of zooplankters from ciliates to copepods. In L. Vörtsjärvi the main food items of perch larvae have been ciliates, rotifers and copepod nauplii and in Väinameri Sea ciliates, copepods and nauplii. Byström and García-Berthou (1999) found in their experiments that perch larvae preferred cyclopoid copepods and nauplii over cladocerans and that they were able to shift to larger prey items earlier compared to roach (*Rutilus rutilus* L.) larvae. In addition, Persson et al. (2000) found a higher proportion of cyclopoid copepods in the diet of 0+ perch compared to roach and reckoned that perch can better cope with copepods' substantial escape abilities. It is well known that zooplankton assemblages in littoral and open water areas differ substantially. It is generally accepted that higher macrophyte coverage is associated with higher zooplankton diversity and abundance (e.g., Špoljar et al. 2018). Considering that as a rule eutrophic lakes harbour higher zooplankton abundances than oligotrophic waters, it can be assumed that 0+ perch returns to the littoral sooner in oligotrophic lakes because zooplankton numbers in pelagic zone are the depleted sooner than in eutrophic waters.

Despite perch larvae regularly inhabiting both littoral and pelagic areas of lakes there is currently no distinct understanding how these different environments influence their zooplankton consumption. Studies conducted in the shallow Väinameri Sea revealed that perch larval zooplankton intake might be higher and their condition factors better in vegetated areas (Zingel et al. 2019a). In lakes, corresponding studies are lacking.

Therefore, the aim of the current study was to assess if there are any differences in the feeding patterns of perch

larvae in different lake habitats. We studied simultaneously the feeding of perch larvae in littoral and pelagic habitats of four different temperate lakes in Estonia and Latvia in spring (2019). Attention was paid particularly to the question of how does the larval food composition differ in the pelagic and littoral zones. We hypothesized that the consumption of zooplankton is higher in vegetated areas as generally there is more diversity and a higher abundance of relevant prey items in the littoral zone.

2. MATERIALS AND METHODS

Studies were carried out once in spring 2019 in four different temperate lakes, one located in Latvia (L. Auciema) and three in Estonia (L. Akste, L. Kaiavere, L. Prossa) (Fig. 1). In general, the studied lakes were relatively small (except L. Kaiavere) and shallow (mean depth < 3 m, max depth < 5 m) (Table 1). Surveys were conducted on 8 May in L. Auciema and on 6 June in lakes Akste, Kaiavere and

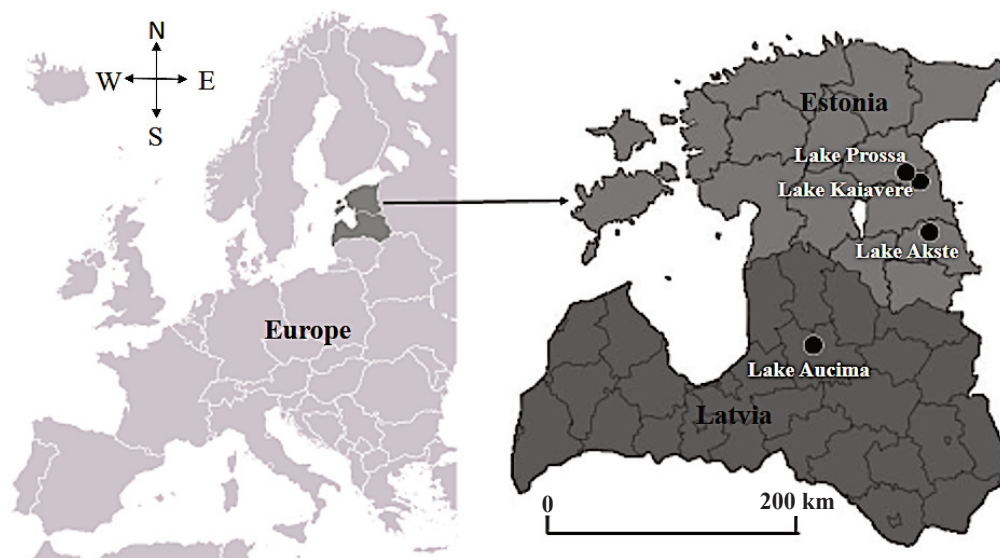


Fig. 1. Location of the studied lakes in Estonia and Latvia (marked by black dots).

Table 1. Characteristic morphological and physico-chemical features of studied lakes in spring, 2019

Lake	Auciema		Akste		Kaiavere		Prossa	
	Littoral	Pelagic	Littoral	Pelagic	Littoral	Pelagic	Littoral	Pelagic
Study time	08.05.2019		06.06.2019		06.06.2019		06.06.2019	
Lake type	II (LV)		IV (EE)		II (EE)		II (EE)	
Surface area (ha)	75.5		5.5		248		24.2	
Mean depth (m)	2.3		–		2.8		2.2	
Maximum depth (m)	4.4		4.3		5.0		4.2	
Water colour	Greenish-yellow		Redish-brown		Brownish-green		Greenish-yellow	
Temperature (°C)	12.27	11.50	23.0	20.10	20.05	17.68	20.05	17.78
Secchi depth (m)	0.7	1.6	0.5	0.7	0.5	1.4	1.0	2.3
Total phosphorus (mg/L)	0.02	0.03	0.028	0.018	0.003	0.003	0.003	0.003
Total nitrogen (mg/L)	1.05	1.02	0.87	0.81	1.68	1.52	1.23	1.19
Oxygen content (mg/L)	12.60	12.87	8.65	8.3	11.97	8.80	14.68	13.75
Oxygen saturation (%)	118.20	118.80	101.1	92.3	131.65	93.3	163.25	146.53
pH	8.79	8.79	6.07	5.67	8.43	8.28	8.36	8.13
Conductivity (µS/cm)	356.83	356.40	19.05	18.83	419.3	422.95	365.05	344.58

Abbreviations: II (LV) – very shallow brown-water lake with high water hardness,

IV (EE) – softwater brown-coloured lakes,

II (EE) – shallow lakes with medium water hardness.

Prossa, to collect and analyse planktonic (ciliates, metazooplankton) and larval fish samples from two habitats of the lakes – littoral (an inshore area covered with macrophytes, depth < 2 m, distance from the shoreline < 50 m) and pelagic (an open water column without aquatic vegetation, depth > 2 m, distance from the shoreline > 50 m), for details see Table 2. The information concerning lakes' macrophyte coverage is given in Table 3 and fish communities in Table 4. All lakes were sampled in the afternoon (12.00–15.00). As the gut passage time for fish larvae is usually considered to be four hours and feeding starts after the sunrise (Sutela and Huusko 2000), the analysed larvae had had enough time to feed and must have been comparable considering their stomach contents. From each lake, two samples per planktonic group were collected: one from the littoral and one from the pelagic habitat. During sampling, also physico-chemical parameters were recorded from both habitats. Plankton (ciliates, metazooplankton) and water chemistry samples were collected and analysed from depth-integrated lake water (with 0.5 m interval) using a Ruttner water sampler. Ciliate and metazooplankton community indices (taxonomic composition, total abundance and biomass) were determined from acidified Lugol's fixed samples using Utermöhl (1958) technique (counting chambers) via inverted microscopy and Bogorov's chambers by stereomicroscopy, respectively (Table 2). All protozooplankters were determined at least to the genus level, metazooplankters to the species level.

Larval fish communities were also sampled once in spring using a conical bongo net (mouth diameter 50 cm, mesh size 0.5 mm) in the pelagic and a scoop-net (mouth diameter 40 cm, mesh size 0.5 mm, equipped with a 2 m handle) in the littoral areas of the lakes by drawing the nets through the habitat's water column (Table 2). Caught larval fish species were identified according to Koblitskaya (1981), measured (total length) and weighed. Larval developmental steps were identified according to Koblitskaya (1981) and Peñáz (2001). Larval fish samples collected with different methods were further preserved in ethanol to estimate larval fish diet. Fish larvae were killed according to EU legislation (Council Regulation 2009), Estonian and Latvian animal welfare laws, guidelines, and policies; appropriate permits for animal collections and animal welfare issues were sought and approved by the local committees. Fish were euthanized with an overdose of ethanol (20 mL/L) before immersing them into the preservative concentration of ethanol (70%) (AVMA 2020). Fish gut content methodology via epifluorescence microscopy (Fukami et al. 1999; Sutela and Huusko 2000) was used to assess the diet of 0+ fish larvae. Larval fish feeding particularly on ciliates was calculated on the basis of first gut quarter methodology (Table 2) as suggested by Zingel et al. (2012). All found food objects were measured

using calibrated oculars (Nikon Eclipse Ti-U; Nikon Instruments Europe B.V., Amstelveen, the Netherlands; 400× magnification). The wet weight of each metazooplankter was calculated based on its length using the Ruttner-Kolisko (1977) formula for rotifers and the Studenikina and Cherepakhina (1969) and Balushkina and Winberg (1979) formulae for cladocerans and copepods. For ciliates biovolumes were estimated by assuming simple geometric shapes and the reconstructed gut contents were calculated as wet weight biomass assuming the specific gravity to be 1.0 g mL⁻¹ (Finlay 1982).

To evaluate larval fish prey importance, feeding homogeneity and strategies at the population level, we calculated several indices of dietary importance: Hurlbert's standardized niche breadth index (Ba), Ivlev's selectivity index (E) and percent index of food item's relative importance (IRI%).

Feeding selectivity of the fish was assessed using Ivlev's (s)selectivity index, E (Ivlev 1961), to describe the degree of selection or avoidance of certain prey organisms by larvae (index values between -0.3 and +0.3 represent nonselective feeding (Lazzaro 1987)):

$$E_i = (r_i - n_i) \times (r_i + n_i)^{-1}, \quad (1)$$

where r_i is the relative abundance (%) of prey category i in the diet of fish and n_i is the relative abundance (%) of prey category i in the environment.

In order to assess the importance of different prey items in larval diet the food item's relative importance index (IRI) was calculated on the basis of three different indices – numbers (N%), mass (W%) and frequency of occurrence (FO%) according to the formula below, and it shows which food objects are relatively the most important concerning all the three aforementioned indices.

$$IRI = (N\% + W\%) \times (FO\%). \quad (2)$$

The indices N% (percent by number), W% (percent by weight) and FO% (frequency of occurrence) were calculated for each prey item as follows:

$$N\% = 100 \times \sum n_i / \sum n, \quad (3)$$

where n is the total number of all food items in the gut contents and n_i is the number of food category i ;

$$FO\% = 100 \times \sum n_i / \sum n, \quad (4)$$

where n is the number of all fish examined and n_i is the number of fish in which prey species i occurred;

$$W\% = 100 \times \sum n_i / \sum n, \quad (5)$$

where n is the number of all fish examined and n_i is the number of fish in which prey species i occurred.

Table 2. Sampling and laboratory analyses of planktonic food web components in studied lakes

Group	Study time	Indicators	Methods	Details & comments	References
Ciliates	Once in spring, 2019; L. Auciema 08.05.2019; L. Kaiavere, L. Prossa and L. Akste 06.06.2019	Taxonomic composition, total abundance, total biomass	Utermöhl technique / inverted microscopy (400–1000× magnification)	Collection of 250 ml samples from integrated lake water; subsamples 50 ml, fixed with acidified Lugol's solution (0.5% of final conc.); for biomass calculations, the first 20 measurable individuals from each taxon measured, specific gravity was assumed to be 1.0 g/ml, biomass expressed in wet weights	Utermöhl 1958; Finlay 1982
Metazooplankton	Once in spring, 2019; L. Auciema 08.05.2019; L. Kaiavere, L. Prossa and L. Akste 06.06.2019	Taxonomic composition, total abundance, total biomass	Bogorov's chambers / stereo- microscopy (80× magnification)	Collection of 10 L sample from integrated lake water, filtered through a 48 µm plankton net; subsamples 50 ml, fixed with acidified Lugol's solution (0.5% of final conc.); for MZP biomass calculations, at least the first 20 individuals from each taxon measured; the individual weights of rotifers estimated from average lengths according to Ruttner-Kolisko (1977); The lengths of crustaceans converted to wet weights according to Studenikina & Cherepakina (1969) for nauplii, and to Balushkina & Winberg (1979) for other groups.	Ruttner-Kolisko 1977; Studenikina & Cherepakina 1969; Balushkina & Winberg 1979
Fish larvae (sampling)	Once in spring, 2019; L. Auciema 08.05.2019; L. Kaiavere, L. Prossa and L. Akste 06.06.2019	Taxonomic composition, total length, weight	Bongo net in pelagic habitats / scoop net in littoral habitats	Pelagic sampling of larvae by hauling the conical bongo net (mouth diameter 50 cm, mesh size 0.5 mm) horizontally through the water column from boat (approximately at 1 m depth, 10 minutes, ~ 2 m s ⁻¹); littoral sampling of larvae by several random drawings through the water column using a scoop net (mouth diameter 40 cm, mesh size 0.5 mm, equipped with 2 m handle)	Zingel et al. 2019a; 2019b
Fish larvae (diet estimation)	Once in spring, 2019; L. Auciema 08.05.2019; L. Kaiavere, L. Prossa and L. Akste 06.06.2019	Diet of perch larvae (20 analysed specimens from both habitats)	(Fore)gut content methodology, EFM (1000× magnification)	Alimentary tract removed from fish, its content stained with DAPI, filtered onto 0.8µm pore-size isopore filters, fluorescently stained food objects counted via EFM using blue and UV light; fluorescently stained ciliates found in first gut quarter identified by the means of using simultaneously fixed ciliate samples.	Hyslop 1980; Sherr & Sherr 1983; Fukami et al. 1999; Sutela & Huusko 2000; Zingel et al. 2012

Abbreviations: EFM – epifluorescence microscopy, conc. – concentration.

Table 3. Overview of main macrophyte community indices for studied lakes in spring, 2019

Lake	Akste	Kaiavere	Prossa	Auciema
Total number of species	23	22	27	17
Total number of E/F/S	19/4/0	10/5/7	15/4/8	11/3/3
Dominating E	<i>Carex</i> spp.	<i>Phragmites australis</i>	<i>Thelypteris palustris</i> = <i>Typha angustifolia</i> = <i>Phragmites australis</i>	<i>Phragmites australis</i>
Dominating F	<i>Nymphaea alba</i>	<i>Nymphaea alba</i> = <i>Nuphar lutea</i>	<i>Nuphar lutea</i>	<i>Nuphar lutea</i>
Dominating S	–	<i>Fontinalis antipyretica</i>	<i>Chara</i> spp.	<i>Stratiotes aloides</i>
Max. growing depth (m)	1.6	2.5	4	1.8
Coverage (%)	10.7	36.2	34.3	10.1
PVI (%)	8.2	33.4	41.7	17

Abbreviations: E – dominating emergent plant, F – dominating floating-leaved plant, S – dominating submerged plant, PVI – percentage volume infested.

Table 4. Fish community composition in studied lakes

Lake	Taxonomic composition	Total number of species	WPUe (g/per net area)
Akste	pike, perch	2	181.9
Kaiavere	ruffe, bleak, pike-perch, roach, perch, bream, white bream, rudd	8	2643.5
Prossa	rudd, bleak, roach, perch, ide, ruffe, pike-perch	7	1031.4
Auciema	bream, crucian carp, perch, roach, rudd, ruffe, spined loach, sunbleak	8	5831.4

Abbreviations: WPUe – weight per unit effort (g/per net area).

Niche breadth was evaluated using the standardized Hurlbert's niche-breadth index (Ba) (Hurlbert 1978; Krebs 1989), which shows the degree of similarity between resources used by population members and resources available to them in their living environment. Scale 0–1; 1 – population uses all resources in equal proportions (a broad diet), values close to 0 – population uses one resource/few resources exclusively (dietary specialisation). Hurlbert's niche-breadth index was calculated as follows:

$$B = 1 / \sum (f_i^2 / a_i), \quad (6)$$

where B is the Hurlbert's niche-breadth index, f_i is the proportion of fish individuals found using resource i (on the scale of 0–1) and a_i is the proportion of the resource i from the total available resources (on the scale of 0–1).

Standardized Hurlbert's niche-breadth index was calculated as follows:

$$Ba = (B - a_{\min}) / (1 - a_{\min}), \quad (7)$$

where, B is the Hurlbert's niche-breadth index and a_{\min} is the smallest observed proportion of all the resources (minimum a_i).

We also compared the species lists for ciliates and metazooplankton found in littoral and pelagic areas using the Bray–Curtis dissimilarity index (Bray and Curtis 1957):

$$BC_{ij} = 1 - 2C_{ij} / (S_i + S_j), \quad (8)$$

where C_{ij} is the sum of the lesser values for only those species in common between both sites and S_i and S_j are the total number of specimens counted at both sites.

Statistical analyses were performed using STATISTICA 8.0 (StatSoft, Inc. 2007) and R programming language (R Core Team 2020). The differences between Bray–Curtis dissimilarity indices were tested by PERMANOVA (Clarke and Gorley 2006) using the R programming environment for statistical computing. Dissimilarities between littoral and pelagic habitats were assessed by the Mann–Whitney U test (M–W test) using STATISTICA 8.0.

3. RESULTS

3.1. Study site characteristics

Study lakes were mostly small and shallow temperate lakes, belonging to different national lake types (Table 1). The colour of water varied from yellow and green to dark brown and transparency reached up to 2.3 metres. The average concentration of total phosphorus and nitrogen characterized the lakes mostly as mesotrophic or eutrophic (according to different nutrient criteria of lake trophic

status classifications reported by Nürnberg (2001), OECD (1982) and Wetzel (1983). A more detailed overview of morphological and physico-chemical characteristics of the investigated study lakes is given in Table 1.

3.2. Zooplankton

Ciliate biomass was highest in L. Kaiavere (0.18 and 0.13 mg L⁻¹ in littoral and pelagic habitats, respectively) and lowest in L. Akste (0.07 and 0.08 mg L⁻¹) and L. Auciema (0.09 and 0.06 mg L⁻¹). In all the studied lakes the ciliate biomass mainly consisted of large-sized herbivorous species (belonging to the order Oligotrichida, e.g., *Pelagostrombidium* spp., *Limnostrombidium* spp. and *Tintinnopsis* spp), followed by bacterivorous species (e.g., *Uronema* sp., *Cyclidium* sp. and *Halteria* sp.). The share of herbivorous species biomass ranged from 65% (littoral of L. Kaiavere) to 88% (littoral of L. Prossa). Bacterivores showed high abundances (maximum 16.7 cells per mL⁻¹ in littoral of L. Kaiavere) but due to their small size their contribution to biomass was marginal.

Metazooplankton biomass was highest in L. Kaiavere (1.8 and 1.1 g m⁻³ in the littoral and pelagic habitat, respectively) (Fig. 2a) and abundance in L. Prossa (1366 and 2785 ind L⁻¹). Total abundance and biomass of metazooplankton was lowest in L. Akste. Rotifers, *Polyarthra* spp. and *Keratella cochlearis* (G.), comprised the most abundant metazooplankters in studied lakes, followed by the copepod nauplii. Cladocerans formed the highest biomass in L. Kaiavere (littoral 205: ind L⁻¹ and 1.5 g m⁻³; pelagic: 62 ind L⁻¹ and 0.7 g m⁻³), as well as in the pelagic habitats of L. Prossa (63 ind L⁻¹ and 0.3 g m⁻³) and L. Auciema (35 ind L⁻¹ and 0.1 g m⁻³). The most abundant cladoceran species was small *Bosmina longirostris*. In the pelagic habitat of L. Kaiavere also the larger *Daphnia cucullata* (Sars) was present in relatively high numbers (28 ind L⁻¹). Other cladoceran species, *Chydorus sphaericus* (Müller), *Holopedium gibberum* (Zaddach), *Ceriodaphnia* spp. and *Alona* spp., were present only with few individuals. Cladoceran community was most limited in L. Akste (1 and 3 ind L⁻¹ in littoral and pelagic zones, respectively). Copepod communities were most abundant in pelagic habitats of the lakes, being most numerous and forming the largest biomasses in L. Prossa.

Zooplankton fauna was statistically significantly different in the studied habitats (pelagic and littoral) (PERMANOVA, Bray–Curtis dissimilarity; Df = 1; SS = 1.29; R² = 0.69; $p = 0.028$; 9999 permutations).

3.3. Perch larvae

Altogether 162 perch larvae (81 larvae from both habitats) were analysed. From L. Akste 42 larvae and from all the other lakes 40 larvae were dissected. An equal number of

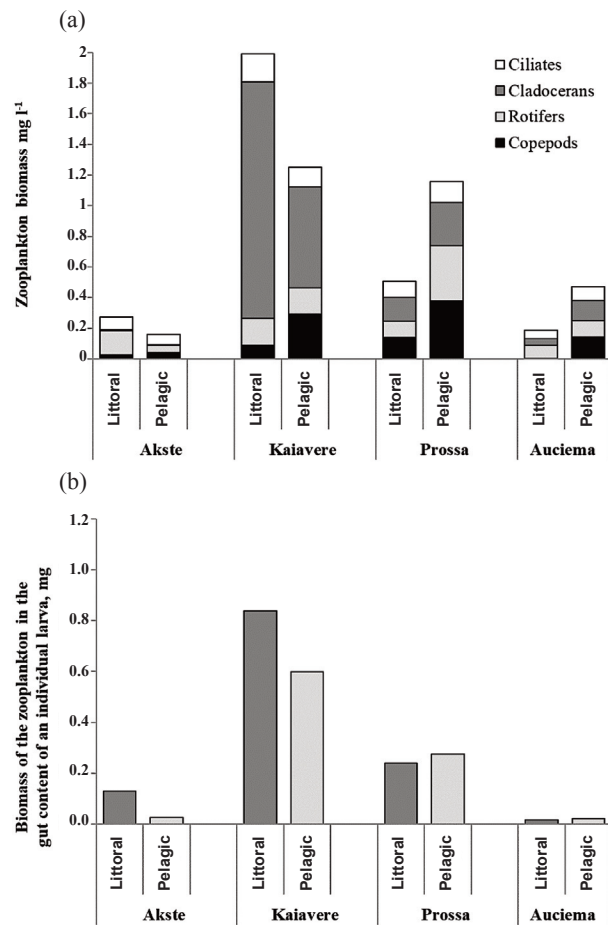


Fig. 2. Zooplankton biomass in (a) littoral and pelagic sites of the lakes and (b) in the gut content of perch larva in spring, 2019.

larvae was analysed from both habitats (Table 5). The Total length and weight of perch larvae was on average 15 mm and 47 mg in pelagic and 16 mm and 59 mg in littoral habitats. The smallest larvae were found in the pelagic habitat of L. Auciema (on average 8 mm and 3.9 mg) and largest in the littoral habitat of L. Akste (on average 20 mm and 97 mg). Considering ontogenetic steps, the larvae in littoral and pelagic zones were always in the

same development stage, indicating therefore also a similar age and making comparison on food consumption between different habitats reasonable. In L. Auciema, larvae were in the developmental stage L2, and in all the other studied lakes in stage L6 (stages defined according to Peňáz 2001). When comparing larval sizes, it should be retained that in L. Auciema larvae were at an earlier stage of development. The total weight of larvae was higher in the littoral than in the pelagic zone in L. Akste (M–W test; $U = 0$; $Z = 5.53$; $p < 0.00001$), L. Kaiavere (M–W test; $U = 0$; $Z = 5.4$; $p < 0.00001$) and L. Prossa (M–W test; $U = 1.5$; $Z = 5.4$; $p < 0.00001$). In L. Auciema the differences were not statistically significant (M–W test; $U = 136$; $Z = 1.72$; $p = 0.85$). The same pattern applied to the larval length: L. Akste (M–W test; $U = 91$; $Z = 3.25$; $p = 0.001$), L. Kaiavere (M–W test; $U = 60.5$; $Z = 3.76$; $p = 0.0002$), L. Prossa (M–W test; $U = 55.5$; $Z = 0.9$; $p = 0.0001$), L. Auciema (M–W test; $U = 180$; $Z = 0.53$; $p = 0.60$).

3.4. Larval diet

The amount of zooplankton biomass consumed by perch larvae was highest in L. Kaiavere and lowest in L. Auciema (Fig. 2b). Again, it should be retained that in L. Auciema larvae were at an earlier stage of development. We found statistically important relation between zooplankton biomass in the lake and zooplankton biomass consumed by fish larvae (linear regression, all lakes and habitats included; $n = 8$; $R^2 = 0.89$; $F = 49.0$; $p = 0.0004$). In L. Akste, L. Kaiavere and L. Prossa the most important food items in terms of zooplankton biomass were cladocerans and in L. Auciema copepod nauplii (Fig. 3). Ciliates were consumed only in L. Akste (both in littoral and pelagic habitat) and L. Auciema (only in littoral). The share of ciliates in larval perch diet was in a good accordance with the share of ciliates in total zooplankton (linear regression, all lakes and habitats included; $n = 8$; $R^2 = 0.94$; $F = 93.1$; $p = 0.00007$). Ciliates were consumed only if their share in the total zooplankton biomass was more than 40%. In all the lakes larvae consumed also small unidentified insect larvae but their relative importance was marginal. Ciliates were also the only zooplankton group

Table 5. The number of analysed perch larvae (n), their total length (TL) with standard deviation, and mean weight (W) with standard deviation in littoral and pelagic habitats of studied lakes

Lake	Akste		Kaiavere		Prossa		Auciema	
	Littoral	Pelagic	Littoral	Pelagic	Littoral	Pelagic	Littoral	Pelagic
Fish (n)	21	21	20	20	20	20	20	20
W (g)	96.6 ± 2.1	80.5 ± 1.5	80.6 ± 0.9	55.3 ± 1.3	54.2 ± 3.0	45.1 ± 2.9	4.0 ± 0.2	3.9 ± 0.3
TL (cm)	20.0 ± 1.2	18.9 ± 0.7	18.1 ± 0.7	17.1 ± 0.6	17.0 ± 0.6	16.1 ± 0.6	8.0 ± 0.6	7.9 ± 0.6

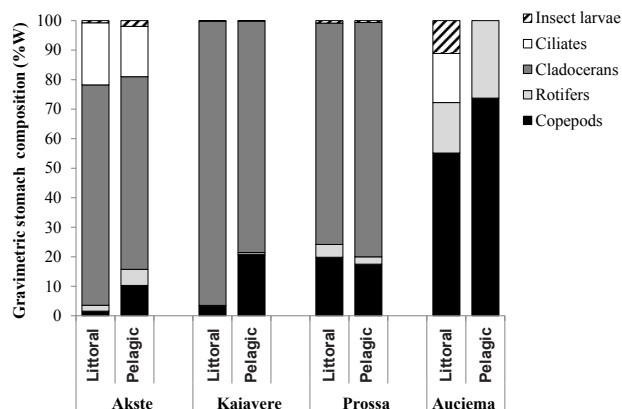


Fig. 3. Gravimetric stomach composition of 0+ perch larvae in littoral and pelagic sites of studied lakes in spring, 2019.

that was always negatively selected (Table 6), considering Ivlev's feeding selectivity index. Cladocerans were positively selected in L. Akste, L. Kaiavere and L. Prossa but totally avoided in L. Auciema. Nauplii and copepodites were mainly positively selected. Selectivity for rotifers showed greatest variability amongst studied lakes (Table 6). According to the IRI index (Table 7) the most important food objects for larval perch were *Bosmina longirostris* (in L. Prossa and in the littoral of L. Kaiavere), *Chydorus sphaericus* (in the pelagic zone of L. Kaiavere), copepod nauplii (in L. Auciema) and ciliates (in L. Akste). According to the Hurlbert's standardized niche breadth the narrowest feeding niche for perch larvae was found in the littoral habitat of L. Akste (Fig. 4) and the widest in the pelagic area of L. Auciema. In all the studied lakes the niche breadth was wider in the pelagic zone than in the littoral.

Table 6. Ivlev's (s)electivity index (E) of larval perch in studied lakes in spring, 2019

Lake	Auciema		Akste		Kaiavere		Prossa	
	Littoral	Pelagic	Littoral	Pelagic	Littoral	Pelagic	Littoral	Pelagic
Ciliata	-0.31	-1	-0.23	-0.25	-1	-1	-1	-1
<i>Polyarthra</i> spp.	0.68	0.57	0.48	0.89	-0.73	0.34	-0.80	-0.73
<i>Keratella cochlearis</i>	-0.06	-0.43	0.64	0.92	0.23	-0.40	-0.91	-0.79
<i>Trichocerca</i> sp.	-1	-	-1	-1	-1	-	0.81	0.12
<i>Bosmina longirostris</i>	-1	-1	0.997	1	0.52	0.80	0.97	0.89
<i>Chydorus sphaericus</i>	-1	-1	-	-	0.98	0.97	-1	-
<i>Holopedium gibberum</i>	-	-	1	0.95	-	-	-	-
Nauplii	0.98	0.67	0.73	0.74	0.15	0.74	0.19	-0.05
Copepodites	-	-1	-1	-1	0.78	0.71	0.93	0.93

Numbers in bold indicate either negative (<-0.3) or positive selectivity (>0.3); - = zooplankton species not present in the selected lake habitat.

Table 7. Percent index of food item's relative importance (IRI%) of larval perch in studied lakes

Lake	Auciema		Akste		Kaiavere		Prossa	
	Littoral	Pelagic	Littoral	Pelagic	Littoral	Pelagic	Littoral	Pelagic
Ciliata	29.4	0	40.3	38.7	0	0	0	0
<i>Polyarthra</i> spp.	19.0	30.2	8.4	9.1	2.4	5.0	2.2	2.3
<i>Keratella cochlearis</i>	6.7	13.1	2.4	7.9	3.4	2.4	0.9	2.3
<i>Trichocerca</i> sp.	0	-	0	0	0	-	6.2	3.3
Rotatoria sp.	-	-	-	-	1.9	3.5	4.8	4.2
<i>Bosmina longirostris</i>	0	0	37.5	30.6	58.0	24.8	56.2	59.6
<i>Chydorus sphaericus</i>	0	0	-	-	25.6	43.0	0	-
<i>Holopedium gibberum</i>	-	-	9.8	4.3	-	-	-	-
Nauplii	42.7	56.7	0	0	5.6	3.1	8.5	8.3
Copepodites	-	0	0	0	3.1	18.2	21.1	19.9
Insecta	2.2	0	0.1	0.2	0.04	0.03	0.1	0.1

- = zooplankton species not present in the selected lake habitat.

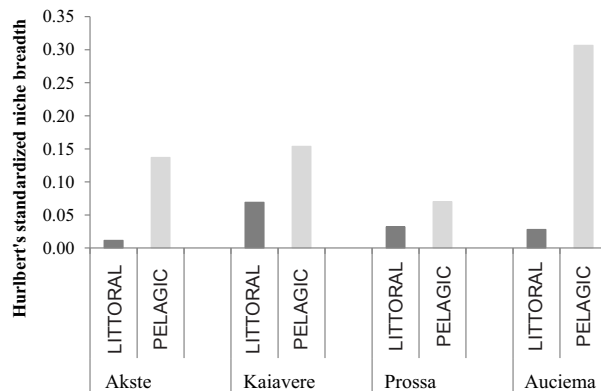


Fig. 4. Values of Hurlbert's standardized niche breadth index (BA) estimated for 0+ perch larvae inhabiting littoral and pelagic areas of lakes Akste, Kaiavere, Prossa and Auciema in spring, 2019.

4. DISCUSSION

4.1. Larval size, food preference and prey importance in different habitats

In the current study the precise moment of larval hatching was not known and we were not able to determine the exact age of perch larvae. Still, the larvae caught from the same lake but from different habitats were always in the same developmental stages. This indicates that larval age and hatching time must have been similar, making comparison on food consumption between littoral and pelagic areas justified. We found that the total length and weight of perch larvae were on average larger in the littoral areas. We cannot entirely rule out the possibility that larger larvae had just recently migrated from the pelagic area back to the littoral and that their bigger size was not related to the different feeding conditions in the littoral area. That kind of migration is common to all perch populations (Urho 1996). In the current study, we found perch larvae in both habitats in all the studied lakes. As we were not able to estimate larval abundance in the littoral, it was not possible to compare the distribution patterns between different habitats quantitatively. Nevertheless, during sampling more larvae seemed to occur in the littoral habitats in the midst of macrophyte stands.

We found that the amount of zooplankton biomass consumed by perch larvae was highest in L. Kaiavere (Fig. 2b). In this lake, the biomass of the most preferred small cladoceran *Bosmina longirostris* was the highest among the studied lakes. Generally, we found statistically important relations between zooplankton biomass in the lakes and zooplankton biomass consumed by fish larvae. This indicates that perch larvae can take advantage of the high zooplankton abundances that occur occasionally in

some lakes – if prey numbers are high their capture rate is high as well.

Cladocerans were the most favourite food in all lakes except L. Auciema where perch larvae preferred copepod nauplii. It is presumed that planktivorous fish prefer cladocerans to copepods (Guma'a 1978; Keast 1977; Skrzypczak et al. 1998), due to differences in motion and escaping abilities. It was mainly so also in the current study both in the littoral and the pelagic habitats. Cladocerans were positively selected in L. Akste, L. Kaiavere and L. Prossa but totally avoided in L. Auciema. In L. Akste, L. Kaiavere and L. Prossa they were also the most important food items as per consumed biomass. In L. Auciema perch larvae preferred copepod nauplii. The reason for former was probably the small size of perch larvae in L. Auciema (total length on average 8 mm) and the gape limitation, which made copepod nauplii and rotifers more suitable prey items. A study in L. Windermere found that the very first food for perch larvae were cyclopoid nauplii, rotifers, algae and ciliates (Guma'a 1978), and in L. Maroz in northern Poland rotifers (especially *Asplanchna priodonta* (Gosse) and *Keratella cochlearis*) were initially the most important (Skrzypczak et al. 1998). Studies by Skrzypczak et al. (1998) and Treasurer (1990) suggest that perch larvae start to feed on cladocerans only when reaching the total length of 9.2 and 11 mm, respectively, which is larger than the larvae in L. Auciema in the current survey. Cladocerans were most favoured also in L. Akste where their abundance in the surrounding environment was very low, indicating highly selective feeding. This also indicates how essentially important is the presence of cladocerans in that stage of larval ontogenetic development.

Ciliates were eaten by perch larvae but they were the only zooplankton group that was always negatively selected for (considering Ivlev's feeding selectivity index). Ciliates were consumed only in L. Akste (in both the littoral and the pelagic zone) and L. Auciema (the littoral) (Fig. 3). Again, in L. Auciema the consumption of ciliates can be explained with the small larval size and in L. Akste by the generally low abundance of suitable food objects. Still it is much more probable that the reason for ciliate consumption was their relatively high share in total zooplankton biomass. Ciliates were consumed only if their share in the total zooplankton biomass was more than 40%, and we found a good accordance in the share of ciliates in total zooplankton and the share of ciliates in larval perch diet. That kind of pattern is also described in our former studies (Zingel et al. 2019a; 2019b) – in L. Vörtsjärvi and the semi-closed Väinameri Sea the ciliates formed a steady part in larval diet if their contribution to total zooplankton biomass exceeded 40%. This most likely also applies to other waterbodies – if the amount of ciliates is reasonably high in the environment, larvae start to utilize this resource, as ciliates, despite their small size, are easily

captured and digested. Still, the consumption of ciliates may remain undetected even in the waterbodies where the former conditions are met due to methodological difficulties.

According to the IRI index (Table 7) the most important food objects for larval perch were *B. longirostris* (in both the littoral and the pelagic habitats of L. Prossa, L. Akste and in the littoral of L. Kaiavere), *Chydorus sphaericus* (in the pelagic area of L. Kaiavere), copepod nauplii (in L. Auciema) and ciliates (in L. Akste). *B. longirostris* and *C. sphaericus* are similarly sized cladocerans (in the current study, 240–350 µm) and evidently represented the suitably sized and shaped objects for larval ingestion at this stage. Rotifers were generally not important, except in L. Auciema; ciliates, again, were important only if they formed a considerable amount of the total zooplankton biomass.

Large-sized cladocerans and spiky and/or hard-bodied rotifers were avoided and were not consumed by perch larvae. Despite there being a considerable amount of *Daphnia cucullata* in pelagic plankton in L. Kaiavere, none of the larvae had ingested these relatively large cladocerans (average length 700 µm) with a long caudal spine. It seemed that both the zooplankters' body shape and size were driving the choices of larval fish (Bremigan et al. 2003, Bremigan and Stein 1994, Mayer and Wahl 1997). Among rotifers, the species with long spines, such as *Kellicottia longispina* (Kellicott), *Filinia longiseta* (Ehrenberg) and also *Keratella quadrata* (Müller) were also not included into larval diet. *Keratella cochlearis* with a smaller body and shorter spines always contributed to the diet although it was not always the preferred object, except for L. Akste. Contrary to the above-mentioned hard-spine rotifers, the soft-bodied *Polyarthra* was selected in L. Auciema by small larvae and in L. Akste, where the food items were limited, but was generally avoided in other lakes where abundant populations of preferred small cladocerans occurred.

4.2. Littoral as food-rich nursery for perch larvae

The food for perch larvae was the most abundant in littoral habitats while their feeding niche in the littoral was always narrower than that in the pelagic area. We found that the zooplankton taxonomic composition was different in the habitats with generally a higher number of species in the littoral habitat. Moreover, according to the Hurlbert's standardized niche breadth the narrowest feeding niche for perch larvae was always found in the littoral area (Fig. 4). It does not mean that in the littoral the variety of suitable food objects was poor. It rather indicates that in the littoral, the perch larvae were able to find certain desired food items in greater numbers and it was unnecessary for them to search for alternative prey items. In the pelagic habitat, perch larvae were forced to eat what they

could find and capture, thus being less specialized than their littoral compatriots. Similarly, studies in L. Itasca, Minnesota, showed that the most plentiful food for fish larvae was in the littoral habitat, whereas in the pelagic zone zooplankton were less abundant and smaller in size than zooplankton in the littoral sites (Whiteside et al. 1985).

Another important issue is the nutritional quality of zooplankton in littoral and pelagic areas as that is the key factor sustaining larval growth. Masclaux et al. (2014) assessed the fatty acid composition of epiphyton and seston in the macrophyte rich littoral zone. They found that the epiphyton that can possibly provide an important dietary source for cladocerans in the littoral had higher content of nutritionally essential compounds of polyunsaturated fatty acids (PUFA) compared to the seston. PUFA are one of the main factors determining food quality for zooplankton and also for fish (Arts et al. 2001; Müller-Navarra et al. 1997; Sargent et al. 1999). Thus, although the larvae generally preferred the same food objects in both habitats, the littoral zooplankton can provide higher quality food for fish larvae than the pelagic.

We found that larvae in the littoral were slightly bigger compared to the pelagic area. This can possibly be explained by both better feeding conditions and less energy spent on hunting for food. This was supported by the Hurlbert's standardized niche breadth results indicating that the larval food demand was more easily satisfied in the littoral area of all the studied lakes. Inhabiting the littoral may also be advantageous as hiding between the macrophytes allows spending less energy on escaping from the predators (Lauridsen and Lodge 1996; Lehtiniemi 2005; Persson and Crowder 1997). Together the results of the current study implicate that macrovegetation as a habitat can offer perch larvae a more suitable environment for feeding and reviving. Therefore, if aiming for superior perch year-class strength, the removal of macrovegetation does not seem to be a commendable management approach. Still, the question remains, why part of larval population migrates into the pelagic zone when the feeding conditions are better in the littoral. It is possible that despite better hiding places and feeding conditions, the littoral has also higher predator density (Urho 1996). Moreover, the competition may be much fiercer in the littoral (Urho 1996). These aspects must be addressed in further studies.

5. CONCLUSIONS

We found that, generally, larval perch food composition was similar in littoral and pelagic habitats – the larvae preferred the same prey items and preyed upon species that were more abundant in the surrounding water. The amount of the consumed zooplankton biomass was not

related to a specific habitat – larvae could take advantage of the large zooplankton biomasses that occurred occasionally in some lakes. The feeding niche was narrower in littoral habitats due to more selective feeding by perch larvae; in the pelagic zone, the consumed food items were more diverse because of the shortage of generally desired prey. We suggest that in pelagic habitats more energy could have been spent on finding and consuming suitable food objects. The results showed that larval length and weight were slightly higher and body conditions better in the littoral habitats of the lakes. Still, it is difficult to make extensive conclusions based on quite limited data available. We found that perch larvae consumed more zooplankton in the littoral habitat but confirming that as the most important factor leading to their bigger size needs further examination and longer time series in different environments.

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Ahvena *Perca fluviatilis* L. vastsete toitumine parasvöötme järvede litoraalis ja pelagiaalis

Katrit Karus, Matiss Zagars, Helen Agasild, Tõnu Feldmann, Arvo Tuvikene,
Linda Puncule ja Priit Zingel

Käesolevas töös uuriti ahvena *Perca fluviatilis* L. vastsete toitumist nelja järve (Auciema, Akste, Kaiavere ja Prossa) litoraalis ja pelagiaalis. Kokku analüüsiti 162 vastset (mõlemast biotoobist 81) selgitamiseks nende toidu koostist. Põhiline tähelepanu oli suunatud küsimusele, kuidas toitumine litoraalis ja pelagiaalis erineb. Tööhüpotees oli, et litoraalis süüakse zooplanktonit rohkem ja vastsed on suuremad. Uuriti toitumist nii proto- (ripsloomad) kui ka metazooplanktonist ja arvatati mitmeid toitumisindekseid (nt Hurlberti toitumisiinži laiuse indeks ja Ivlevi valivusindeks) leidmaks vastsete olulisemaid toiduobjekte ja selgitamiseks toitumismustrite erinevusi. Tulemused näitasid, et järvede litoraalis oli vastsete pikkus, mass ja tüsedus veidi suurem kui pelagiaalis. Toitumisiinži oli litoraalis kitsam, mis võib viidata parematele toitumistingimustele. Kõige eelistatumad toiduobjektid olid üldjuhul väikesed vesikirbud (*Bosmina longirostris* Müller). Ainurakseid ripsloomi üldiselt välditi ning söödi üksnes juhul, kui nende osakaal kogu zooplanktoni biomassis oli suurem kui 40%. Samas võivad ainuraksed olla vastsete jaoks väga olulised tingimustes, kus vesikirbuliste arvukus on madal.